The 7th international symposium on earthworm ecology · Cardiff · Wales · 2002

Population dynamics of ambient and altered earthworm communities in row-crop agroecosystems in the Midwestern U.S.

William D. Shuster^{1*}, Martin J. Shipitalo², Patrick J. Bohlen³, Scott Subler⁴ and Clive A. Edwards⁵

- ¹ United States Environmental Protection Agency (USEPA) NRMRL SEB ML498, 26 W, Martin Luther King Drive, Cincinnati OH 45268, USA
- ² USDA-ARS North Appalachian Experimental Watershed, Coshocton OH 43812, USA
- ³ MacArthur Agro-Ecology Research Center, Archbold Biological Station, 300 Buck Island Ranch Road, Lake Placid FL 33852, USA
- ⁴ Pacific-Garden, 104 Mill Street, Millheim PA 16854, USA
- ⁵ 1735 Neil Avenue, The Ohio State University, Columbus OH 43210, USA

Submitted September 6, 2002 · Accepted May 15, 2003

Summary

Earthworms affect agroecosystem processes and few studies have addressed population dynamics when earthworms are intentionally introduced. Handsorting and formalin extraction were used semi-annually from fall 1994 to fall 1997 to measure populations in plots with and without added earthworms under chisel till in a corn-soybean rotation (CT) and a ridge-till system in a corn-soybean-wheat rotation (RT) in Ohio, USA. Earthworm communities were altered by adding ~76 Lumbricus terrestris (L.) m⁻² each spring and fall into plots with no, or very few of these anecic earthworms. Increases in *L. terrestris* were small (~7 m⁻²) compared to the number added and their establishment was at the expense of the epigeic earthworm *L. rubellus* (Hoff.), which declined four and two-fold in CT and RT, respectively. Populations of the endogeic earthworm *Octolasion tytaeum* (Sav.) were unaffected by the addition of *L. terrestris*. Sampling 5 years after the additions indicated that *L. terrestris* persisted only in the RT plots. The decline in *L. rubellus* populations in plots with added anecic worms was no longer evident. We understand that the increased number and amounts of residues and the minimal level of disturbance found in RT probably increased the extent and quality of earthworm habitat over CT plots, which had fewer crops, less cover, and periodic disturbance. Apparently, population dynamics and competitive relationships among different earthworm functional groups were regulated by agroecosystem type, and their correspondent disturbance regimes and resource distributions.

Key words: Earthworms, Lumbricus terrestris, population dynamics, carrying capacity

^{*}E-mail corresponding author: shuster.william@epa.gov

Introduction

Earthworms constitute a major proportion of the soil faunal biomass in many agroecosystems. By burrowing, foraging, and casting earthworms modulate resource distribution, shift biogeochemical pathways, and alter soil structure; in effect engineering an interface between the biotic and abiotic aspects of the soil. Disturbance in the form of tillage or other crop management practices, however, can alter patterns of growth, reproduction, and both inter and intraspecies interactions (Springett et al. 1992). In many instances, a disturbance or shift in food source and soil habitat will increase the plasticity of earthworm ecological groups (i.e., anecic, epigeic, endogeic) or narrow the overlap between behaviors of different species (Neilson et al. 2000).

Lumbricus terrestris (L.) is an anecic species that forms semi-permanent vertical burrows and consolidates coarse organic litter from the soil surface into its burrows. Consequently, it plays a major role in regulating food distribution and availability for other species (Bohlen et al. 1995; Shuster et al. 2001). Lumbricus rubellus (Hoff.) belongs to the epigeic group, that typically forage within the litter layer and burrow in the upper 10 cm of soil. Depending on soil and litter conditions, the habitats of anecic and epigeic species can overlap in the litter layer. The larger size and burrowing behavior of anecic earthworms gives them more flexibility than epigeic species in modifying their habitat. Endogeic earthworms inhabit the soil matrix and consume soil as they develop more or less horizontal burrow networks at depths of up to 15 cm. Although endogeic species do not typically overlap with anecic or epigeic earthworms, anecic species may enhance resource availability to endogeic species by incorporating surface organic matter into the soil matrix (Shaw & Pawluk 1986; Shuster et al. 2001).

Thus, the interaction between crop management practices and the predominance of certain ecological groups will likely affect the structure of the earthworm community in agroecosystems. Our objective was to investigate the effects of cropping systems and the introduction of deep-burrowing earthworm species on earthworm community structure and population dynamics.

Materials and Methods

Earthworm community dynamics were investigated in plots with and without added earthworms established at the Ohio Management Systems Evaluation Area (MSEA) (Ward et al. 1994) near Piketon, Ohio. Soils at

this flood plain site are predominantly Huntington silt loam (fine-silty, mixed, active, mesic Fluventic Hapludoll). The upper 15 cm of this soil had an average organic carbon content of 1.6 % and was 21 % sand, 55 % silt, and 24 % clay. Precipitation averaged 900 mm yr⁻¹ and the water table was rarely deeper than 2 m.

A corn (*Zea mays* L.)-soybean (*Glycine max* Merr.) chisel-till rotation (CT), and a corn-soybean-winter wheat (*Triticum aestivum* L.)-hairy vetch (*Viccia villosa* L.) cover-crop ridge-till rotation (RT) were established in 1991. The CT corn crop was sown with a notill planter into soybean stubble and the soil was chiseled to 25 cm then disked twice to 10 cm prior to planting soybean. The RT system was based on 20-cm high ridges formed with a ridge-till planter. Corn and soybean were cultivated twice and wheat was drilled on and between the ridges. Vetch was planted after wheat harvest in July and killed with herbicide in the spring before planting corn.

Each management system was replicated three times in 0.4 ha plots. Percent residue cover was measured using 30 m transects with observations made at 30 cm intervals.

Two sets of earthworm treatments were maintained in the plots with one used to monitor earthworm populations and the other for hydrological measurements (Subler et al. 1997). At the start of this study in 1993, no L. terrestris were detected in any of the plots and the ambient communities were composed primarily of the epigeic species L. rubellus and the endogeic species Aporrectodea tuberculata (Eisen), A. trapezoides (Dúges), and A. caliginosa (Savigny). Earthworm additions were made to 6.1×6.1 m enclosures made of corrugated plastic that extended 25 cm above and 5 cm below the soil surface. Each spring and fall, beginning in fall 1993 and ending in fall 1997, earthworms were added at a rate of ~100 individuals m⁻². The earthworms were collected by formalin expulsion (Raw 1959) from a no-till cornfield and 76% were adult and juvenile L. terrestris and the rest were either Aporrectodea or Octolasion spp. (Subler et al. 1997).

Earthworm populations were assessed in the spring and fall of each year from fall 1993 to spring 1997, just prior to the earthworm additions, and again in April 2002, five years after the additions were discontinued. Soil was removed from four $38 \times 38 \times 15$ cm deep pits in each subplot and hand-sorted for earthworms. Afterwards, dilute formalin was added to each pit to expel deep-burrowing earthworms. The earthworms were identified to species (adults) or genus (juveniles) levels (Schwert 1990). Ash-free dry weight (AFDW) was determined by drying the earthworms at 60 °C, weighing them, then re-weighing after ashing in a muffle furnace.

Cropping systems treatments were arranged in a complete randomized block design, with a split plot for

Table 1. Mean earthworm abundance and mean per-capita ash-free dry weight (abundance, ash-free weight) for predominant species of epigeic, endogeic, and anecic species for chisel-till corn-soybean, and ridge-till corn-soybean-wheat agroecosystems, from fall 1994 to spring 1997

	Epigeic (<i>L. rubellus</i>)	Endogeic (<i>O. tyrtaeum</i>)	Anecic (<i>L. terrestris</i>)	Total		
Chisel-Till (CT) †	number m ⁻² , mg individual ⁻¹					
Ambient Addition	15.5a, 89.0a 3.5b, 75.7a	2.0a, 45.0a 2.7a, 61.1a	0.4a, 150.0a 3.6b, 202.8a	17.9a 9.8a		
Ridge-Till (RT)						
Ambient Addition	24.0a, 98.8a 11.8a, 111.9a	5.5a, 76.4a 5.0a, 66.0a	0.4a, 75.0a 6.9b, 365.2b	29.9a 23.7a		

^{*} Means by species in earthworm treatments that are followed by different letters a, b within agroecosystems are significantly different at P < 0.05.

Table 2. For comparison purposes, spring-only 1994–97 and spring 2002 (1994–97, 2002) mean earthworm abundance for the predominant species of epigeic, endogeic, and anecic functional groups are shown for chisel and ridge-till agroecosystems at Piketon OH site. Statistics are indicated for 2002 data

	Epigeic (<i>L. rubellus</i>)	Endogeic (<i>O. tyrtaeum</i>)	Anecic (<i>L. terrestris</i>)	Total		
Chisel-Till (CT)	Individuals m ⁻²					
Ambient Addition	30.5, 33.4a,x 5.2, 33.3a,x	2.2, 14.3a,x 2.2, 0.0b,x	0.8, 0.0a,x 4.4, 0.0a,x	47.7a 33.3a		
Ridge-Till (RT)						
Ambient Addition	45.1, 41.6a,x 22.2, 35.5a,x	9.7, 13.1a,x 3.9, 2.4b,x	0.6, 2.4b,y 8.8, 6.0b,y	57.1a 42.9a		

Means for earthworm treatments followed by different letters a, b within agroecosystems are significantly different at P < 0.05. Means followed by different letters x, y among agroecosystems are significantly different at P < 0.05

earthworm treatment. Repeated measures analysis of variance (ANOVA) was performed on the time series of log-transformed earthworm population data from 1994–1997. Earthworm population data from 2002 was treated as a separate data set. Log-transformed data from the 2002 sampling date was analyzed by two-way ANOVA with agroecosystem and earthworm treatments as main effects and blocks as a random factor (Statistical Analysis System, ver. 8.2; SAS Institute 2002).

Results

Soil water contents averaged 0.35 cm³ (water) cm⁻³ (soil) and conditions were generally favorable at sampling with between zero and 30 mm precipitation before any given sampling. Surface residue cover ranged

from 19 to 66 % in CT and from 25 % under wheat to 95 % under the vetch cover crop in the RT system.

Earthworm populations were highly variable and block effects were generally not significant, although one block had lower overall populations for the duration of the experiment. Population densities of L. terrestris averaged over 1994-1997 were higher in RT than in CT and were significantly greater in addition than in ambient plots in both systems (Table 1). Additionally, L. terrestris in RT were larger than those in CT (Table 1). Likewise, L. rubellus was more abundant in RT than in CT, but these differences were not significant. Numbers of L. rubellus were significantly lower in CT addition plots, but declined to a lesser extent under RT (Table 1). L. rubellus were of similar size in ambient plots for both cropping systems, maximized in RT addition, and were significantly smaller in CT addition than in ambient plots (Table 1). The abundance of endogeic species O. tyrtaeum was similar

[†] There were no significant differences between cropping systems

among agroecosystems and earthworm treatments (Table 1), but they were smaller in CT than in RT plots.

The 5-yr post addition sampling indicated that *L. terrestris* was present only in RT plots (Table 2) and at levels similar to those observed during the addition phase (Table 1). Furthermore, *L. terrestris* were observed in RT ambient plots, although at lower population densities than in addition plots. In RT, *L. terrestris* individuals in the 2002 samples were heavier than those found during the addition phase with average weights of 484 and 571 mg ind⁻¹ in the ambient and addition plots, respectively. The numbers of *L. rubellus* were similar among cropping systems and earthworm treatments (Table 2). Populations of the endogeic earthworm *O. tyrtaeum* were lower in addition plots than in ambient plots for both cropping systems.

Discussion

The cropping regimes significantly influenced earthworm community structure and population density. These effects were likely due to differences in agroecosystem management, which integrates crop type and sequence with tillage. Some differences between agroecosystems include specific resource base and habitat conditions due to crop type, cropping sequence, and residue management; and mechanical disturbance (i.e., tillage) regimes. We considered CT to be a system with higher disturbance and with lower resource availability than RT. In the CT system, tillage was periodic and some crop residues were incorporated into the soil, decreasing their availability to earthworms foraging at the surface. In contrast, the ridge-till system had minimal disturbance and high resource availability due to the permanent ridges and an expanded crop rotation with more persistent cover and greater inputs of higher quality crop residues, which have been shown to increase earthworm populations (Edwards & Bohlen 1996).

We expected that the added earthworms would establish in higher numbers and would be present in both agroecosystems, but the failure of *L. terrestris* to persist in CT suggests that the conditions were not conducive to its survival. Earthworms added to CT may have remained active, but eventually expired from a lack of food resources, extremes in environmental conditions, predation, or other factors. Additionally, their reproductive output may not have been sufficient to sustain the populations anyways. Other workers have found that various methods to introduce non-native earthworm species to agroecosystems either failed (Butt et al. 1999), or did not increase populations as much as expected relative to the numbers of earth-

worms added (Bohlen et al. 1995). The number of *L. terrestris* we measured was only a small proportion of the number added to the plots, suggesting that a relatively large number was necessary to maintain the disproportionately small populations that we observed. The burrowing activities of individuals that were temporarily active, or persisted until after subsequent additions may have increased macroporosity, as indicated by an increase in the amount of water leaching from plots with added earthworms (Subler et al. 1997). These individuals may also have increased short-term residue consumption and incorporation into the soil.

Although we did not explicitly test for intraspecies competition, our addition treatments may have triggered competition among deep-burrowers for scarce resources in the CT system. Given the high numbers of earthworms added, it is likely that some individuals may have dispersed outside of the plots to escape unfavorable conditions related to competitive interactions within and between species. Although L. terrestris populations in the period between 1994–1997 were generally greater in addition plots relative to controls it is questionable whether these populations reached equilibrium at any point during this phase. Our recent sampling indicates that equilibrium abundance, or carrying capacity, for *L. terrestris* was about 7 individuals m⁻² in the RT system where disturbance was minimal and food resources plentiful.

The modest populations of L. terrestris that did establish in both cropping systems during the addition phase did so apparently at the expense of the surfacedwelling species, L. rubellus and to a greater extent in CT than in RT (Table 1). After *L. terrestris* populations went extinct in CT plots, L. rubellus populations apparently recovered and increased to the point that the epigeic populations were nearly equivalent between addition and ambient plots. Under conditions of higher residue availability and variety, the disparity between the earthworm treatments in the RT system narrowed after earthworm treatments were discontinued. There were apparently sufficient resources available in the RT system to maintain viable populations of the major species from anecic and epigeic functional groups and to prevent strong interspecies competition for available resources. Our recent observations also suggest that conditions in the RT system were such that populations of anecic species were viable enough to disperse more than 30 m from addition to adjacent ambient plots. If the earthworm population dispersed 30 m in five years, then the dispersal velocity would be consistent with the average for several species including L. terrestris of 6.3 m yr⁻¹ as observed on a reclaimed polder in the Netherlands (Ligthart & Peek 1997). Although we cannot separate the effects of crop rotation and tillage regime in this experiment, our results indicate that the activity of anecic species is related to an interaction between resource and disturbance regimes in the different agroecosystems studied.

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